LIFE HISTORY AND DESCRIPTION OF IMMATURE STAGES OF *TRUPANEA VICINA* (WULP) (DIPTERA: TEPHRITIDAE) ON WILD AND CULTIVATED ASTERACEAE IN SOUTHERN CALIFORNIA

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Abstract.—*Trupanea vicina* (Wulp) is a multivoltine, narrowly oligophagous fruit fly (Diptera: Tephritidae) mainly infesting flower heads from at least four genera of Asteraceae in the subtribe Pectidinae of the tribe Helenieae, including cultivated marigold (*Tagetes* sp.), in the southwestern United States. The egg, first-, second-, and third-instar larvae, and puparium are described and figured. The egg pedicel has a single row of aeropyles. The integumental petal is fused laterally with the stomal sense organ in the first instar. The interspiracular processes of the first instar are large, broad, and multi-branched, like those of *T. wheeleri* Curran. The lateral spiracular complexes of the third instar are identical to those of *T. imperfecta* (Coquillett) and *T. wheeleri*, but different from nine other California congeners, which in turn differ from each other in type and number of sensilla comprising their metathoracic and abdominal, lateral spiracular complexes. The mouth hooks of the third instar of *T. vicina* are bidentate, not tridentate like 10 other *Trupanea* spp. examined from California. The life cycle of *T. vicina* in southern California is of the aggregative type. Most eggs are inserted between or through the tips of the phyllaries and parallel to and between the florets of closed, preblossom flower heads. The first instars feed within the floral tubes; whereas, the second instars feed mainly in ovules of preblossom flower heads or soft achenes of open heads. Most third instars feed in the centers of open or postblossom flower heads on the soft achenes. Pupariation occurs inside the mature flower heads, from which the adults later emerge. Limited reproduction occurs on wild hosts in southern California, but three to four, overlapping generations are produced on marigold from early summer (June) through November, or until frost. *Pteromalus* sp. (Hymenoptera: Pteromalidae) is reported as a probable solitary, larval-pupal endoparasitoid.

Key Words: Insecta, *Trupanea, Tagetes*, Asteraceae, marigold, nonfrugivorous Tephritidae, biology, taxonomy of immature stages, flower-head feeding, host-plant range, parasitoid

This is the last paper in our recent series on *Trupanea*, one of the larger and more widespread genera of nonfrugivorous fruit flies in North America and California, though of little or no economic importance (Foote and Blanc 1963, Foote et al. 1993). *Trupanea* remained little known (Foote 1960, Foote et al. 1993) until we published detailed life histories of 11 species from southern California (Cavender and Goeden 1982; Goeden 1987, 1988; Goeden et al. 1998a, b; Goeden and Teerink 1997b, 1998, 1999a, b; Headrick and Goeden 1991; Knio et al. 1996b), along with descriptions of

their immature stages (Cavender and Goeden 1982; Goeden et al. 1998a, b; Goeden and Teerink 1997b, 1998, 1999a, b; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). In this paper we describe the life history and immature stages of a twelfth species, *T. vicina* (Wulp). Two additional species, *T. femoralis* (Thomson) and *T. radifera* (Coquillett) remain under study in southern California, but may not be completed and published before RDG retires.

MATERIALS AND METHODS

This study was added to the series on *Trupanea* in 1997 following the discovery in October of an ornamental planting of marigold (*Tagetes* sp.) heavily infested with *T. vicina* just west of the University of California, Riverside, campus. Fortuitously, this discovery was followed by our chance sampling of infested mature flower heads of *Thymophylla* (= *Dyssodia*) *pentachaeta* var. *belenidium* (deCandolle) Strather in Shadow Valley (E Mojave Desert) ca. 13 km W of Mountain Pass at 1,110-m elevation, NE San Bernardino Co., on 6.xi.1997. This latter sample yielded additional specimens of immature stages and adequate data on phytophagy in a wild host plant, which had eluded us since 1991, when our field studies of *T. vicina* first began. Thus, the present study was based in large part on dissections of subsamples of flower heads collected from these two locations in the manner described by Goeden (1985, 1992). One-liter samples of excised, immature and mature flower heads containing eggs, larvae, and puparia were transported in cold-chests in an air-conditioned vehicle to the laboratory and stored under refrigeration for subsequent dissection, photography, description, and measurement. Seventeen eggs, 11 first-, eight second-, and 10 third-instar larvae, and five puparia dissected from flower heads were preserved in 70% EtOH for scanning electron microscopy (SEM). Additional puparia were placed in separate, glass shell vials stoppered with absorbant cotton and held in humidity chambers at room temperature for adult and parasitoid emergence. Specimens for SEM were hydrated to distilled water in a decreasing series of acidulated EtOH. They were osmicated for 24 h, dehydrated through an increasing series of acidulated EtOH and two, 1-h immersions in Hexamethyldisilazane (HMDS), mounted on stubs, sputter-coated with a gold-palladium alloy, and studied with a Philips XL-30 scanning electron microscope in the Institute of Geophysics and Planetary Physics, University of California, Riverside.

Most adults reared from isolated puparia were individually caged in 850-ml, clear-plastic, screened-top cages with a cotton wick and basal water reservoir and provisioned with a strip of paper toweling impregnated with yeast hydrolyzate and sucrose. These cages were used for longevity studies in the insectary of the Department of Entomology, University of California, Riverside, at 25 ± 1°C, and 14/10 (L/D) photoperiod. Three virgin males and two females obtained from emergence cages also were held in each of six, previously unused, clear-plastic, petri dishes provisioned with a flattened, water-moistened pad of absorbant cotton spotted with honey (Headrick and Goeden 1991, 1994) for observations of their courtship and copulation behavior.

Plant names used in this paper follow Hickman (1993) and Bremer (1994); tephritid names and adult terminology follow Foote et al. (1993). Terminology and telegraphic format used to describe the immature stages follow Goeden et al. (1998a, b), Goeden and Teerink (1997b, 1998, 1999a, b), Headrick and Goeden (1991), Knio et al. (1996a), Teerink and Goeden (1998, 1999), and our earlier works cited therein. Means ± SE are used throughout this paper. Voucher specimens of *T. vicina* and its parasitoids reside in the research collections of RDG; preserved specimens of eggs, larvae and puparia are stored in a separate collection of immature Tephritidae acquired by JAT and currently maintained by RDG.

Results and Discussion

Taxonomy

Adult.—*Trupanea vicina* was first described by Wulp (1900) as *Urellia vicina*. It was transferred to *Trupanea* (as *Typanea*) by Hendel (1914). Foote (1965) designated a female from Orizaba, Mexico, now in the Natural History Museum as lectotype. Wulp (1900), Curran (1932), Malloch (1942), Foote (1960), Foote and Blanc (1963), and Foote et al. (1993) pictured the wing pattern of the female and male, which unlike several North American *Trupanea* spp., is not sexually dimorphic (Foote et al. 1993).

Immature stages.—The egg, larvae, and puparium heretofore have not been described nor illustrated.

Egg: Forty-one eggs of *T. vicina* dissected from field-collected flower heads were white, opaque, smooth, elongate-ellipsoidal, 0.72 ± 0.006 (range, 0.64–0.80) mm long, 0.19 ± 0.001 (range, 0.17–0.20) mm wide, smoothly rounded at tapered basal end (Fig. 1A)$_S$ peglike pedicel, 0.02 mm long, circumscribed by single row of oblong-elliptical aeropyles (Fig. 1B), with micopyle in center at apex surrounded by spokelike furrows, which may help channel sperm (Fig. 1C).

Eggs of all 12 species of *Trupanea* from California studied to date are similar in shape, color, and smoothness. Except for *T. bisetosa* (Coquillett) and *T. wheeleri* Curran with one or two rows of aeropyles (Knio et al. 1996a, Goeden and Teerink 1999b), the eggs of *T. vicina* and nine other species of *Trupanea* previously studied have only one row of aeropyles (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al. 1998a, b; Headrick and Goeden 1991; Teerink and Goeden 1998, 1999). The egg of *T. vicina* is longer on average than those of *T. actinobola* (Loew), *T. californica* Malloch, *T. imperfecta* (Coquillett), *T. pseudovicina* Hering, *T. signata* (Foote), and *T. wheeleri* (Goeden et al. 1998; Goeden and Teerink 1997b, 1998, 1999b; Headrick and Goeden 1991; Teerink and Goeden 1998); about as
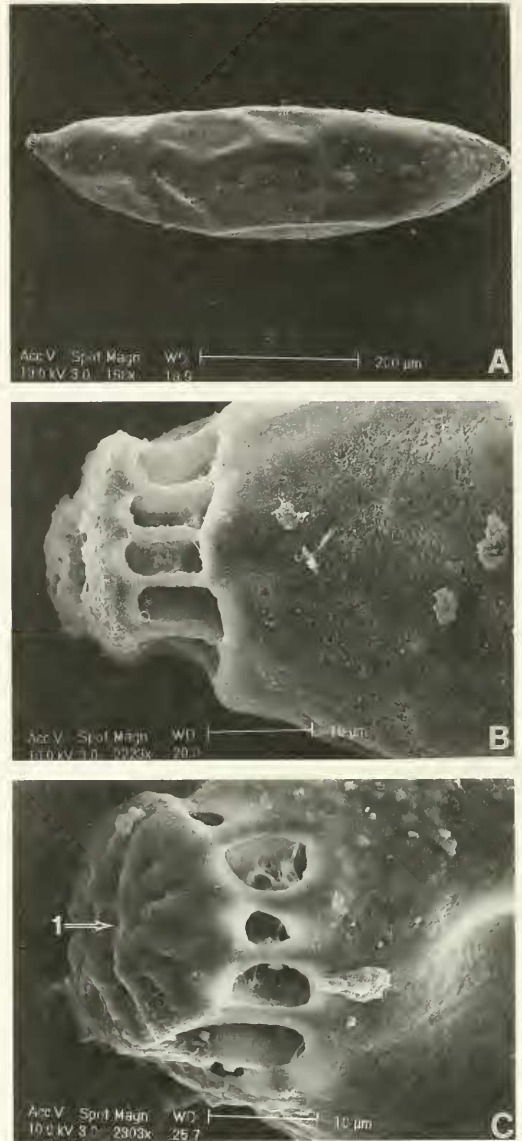

Fig. 1. Egg of *Trupanea vicina*: (A) habitus, anterior end to left; (B) pedicel, aeropyles; (C) pedicel apex, 1-micopyle.

long as those of *T. bisetosa, T. jonesi* Curran, and *T. nigricornis* (Coquillett) (Goeden et al. 1998a, Knio et al. 1996a); and only shorter than the egg of *T. conjuncta* (Adams) (Teerink and Goeden 1998).

First instar: White, elongate-cylindrical, rounded anteriorly and posteriorly (Fig. 2A), minute acanthae circumscribe intersegmental lines; gnathocephalon smooth,
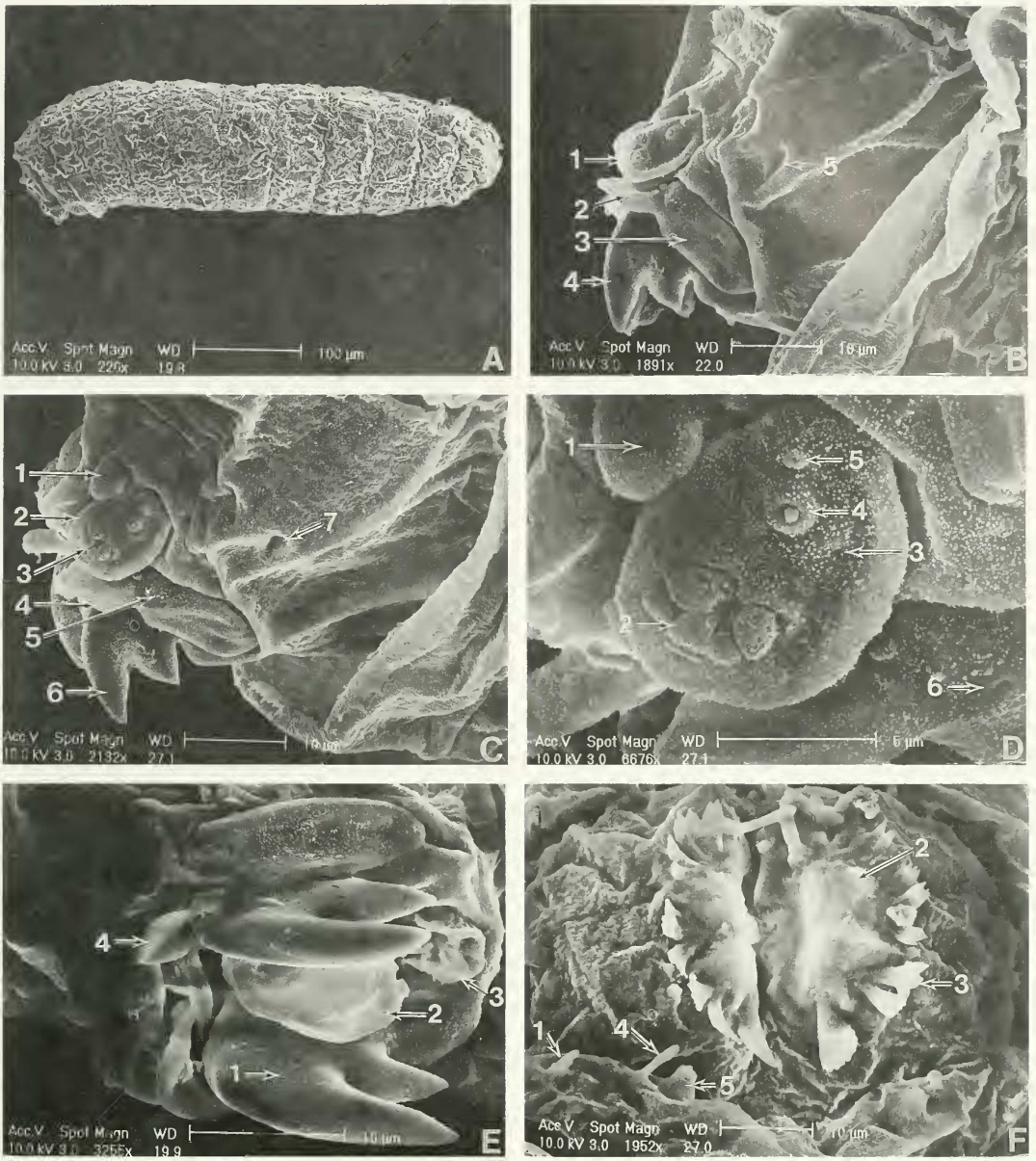
Fig. 2.   First instar of *Trupanea vicina*: (A) habitus, anterior end to left; (B) gnathocephalon, lateral view, 1- anterior sensory lobe, 2- integumental petal, 3- stomal sense organ, 4- mouth hook, 5- pit sensillum; (C) gnathocephalon, dorsolateral view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- integumental petal, 5- stomal sense organ, 6- mouthhook, 7- pit sensillum; (D) anterior sensory lobe, 1- dorsal sensory organ, 2- terminal sensory organ, 3- pit sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- stomal sense organ; (E) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe, 3- labial lobe, 4- integumental petal; (F) caudal segment, 1- stelex sensillum, 2- rima, 3- interspiracular process, 4- intermediate sensory complex, medusoid sensillum, 5- intermediate sensory complex, stelex sensillum.

lacking rugose pads (Fig. 2B, C); dorsal sensory organ a dome-shaped papilla (Fig. 2C-1, D-1); anterior sensory lobe (Fig. 2B-1, C-2, D) bears the terminal sensory organ (Fig. 2C-3, D-2), pit sensory organ (Fig. 2D-3), lateral sensory organ (Fig. 2D-4) and supralateral sensory organ (Fig. 2D-5); stomal sense organ ventrad of anterior sensory lobe (Fig. 2B-3, C-5, D-6); mouth hooks bidentate (Fig. 2B-4, C-6, E-1); median oral lobe laterally flattened (Fig. 2E-2); labial lobe with two pore sensilla (Fig. 2E-3); pair of prominent integumental petals (Fig. 2B-2, C-4, E-4) dorsal to mouth hooks, each integumental petal is fused laterally with stomal sense organ (Fig. 2B-3, C-5); pit sensillum laterad of mouth lumen (Fig. 2B-5, C-7); anterior thoracic spiracle not present; caudal segment with two stelex sensilla dorsad and ventrad (Fig. 2F-1) of posterior spiracular plates; posterior spiracular plate bears two ovoid rimae, ca. 0.006 mm in length (Fig. 2F-2), and four interspiracular processes, each with 1–4, apically multidentated branches, longest measuring 0.008 mm (Fig. 2F-3); intermediate sensory complex consists of a stelex sensillum (Fig. 2F-4) and a medusoid sensillum (Fig. 2F-5).

The first instar is similar in general habitus and sensory structures to previously studied *Trupanea* species, except that the integumental petal is fused with the stomal sense organ (Goeden and Teerink 1997b, 1998, 1999a, b; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Like *T. wheeleri* (Goeden and Teerink 1999b), the interspiracular processes are large, broad, branched, and apically multidentate, and thus are far more elaborate than those of, for example, *T. arizonensis* (Goeden and Teerink 1999a), *T. conjuncta* (Teerink and Goeden 1998), and *T. jonesi* (Goeden et al. 1998a).

Second instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly (Fig. 3A), minute acanthae circumscribe intersegmental lines; gnathocephalon conical (Fig. 3B); dorsal sensory organ a dome-shaped papilla (Fig. 3C-1); anterior sensory lobe (Fig. 3C-2) bears the terminal sensory organ (Fig. 3C-3), lateral sensory organ (Fig. 3C-4), and supralateral sensory organ (Fig. 3C-5), pit sensory organ not shown; integumental petals separated from stomal sense organ (Fig. 3D); mouth hooks bidentate (Fig. 3B-1, C-6, D-1); median oral lobe laterally flattened, apically pointed, and with ventral lobe (Fig. 3C-7, D-2); labial lobe with two pore sensilla (Fig. 3D-3); minute acanthae circumscribe anterior margin of prothorax (Fig. 3B-2, C-8); rugose pads circumscribe prothorax posteriorad to acanthae (Fig. 3B-3, C-9); anterior thoracic spiracle bears three ovoid papillae (Fig. 3E); lateral spiracular complexes not seen; caudal segment with two stelex sensilla, dorsad and ventrad (Fig. 3F-1) of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.02 mm in length (Fig. 3F-2), and four interspiracular processes, each with 1–4 branches, longest measuring 0.016 mm (Fig. 3F-3); intermediate sensory complex consists of a medusoid sensillum (Fig. 3F-4) and a stelex sensillum (Fig. 3F-5).

The interspiracular processes of the second instar are similarly branched, though not as broad as the first instar, and apically pointed, not dentate. Unlike the second instars of *T. nigricornis, T. pseudovicina*, and *T. wheeleri*, the rugose pads laterad of the mouth lumen are not serrate (Goeden and Teerink 1998, 1999b; Knio et al. 1996a).

Third instar: White, barrel-shaped, tapering anteriorly, rounded posteriorly, minute acanthae circumscribe intersegmental lines (Fig. 4A)$_S$ gnathocephalon conical (Fig. 4B), rugose pads laterad of mouth lumen with serrate margins (Fig. 4C-1); dorsal sensory organ a dome-shaped papilla (Fig. 4C-2); anterior sensory lobe (Fig. 4C) bears the terminal sensory organ (Fig. 4C-3), pit sensory organ (Fig. 4C-4), lateral sensory organ (Fig. 4C-5), and supralateral sensory organ (Fig. 4C-6); stomal sense organ prominent ventrolaterad of anterior sensory lobe (Fig. 4C-7); mouth hooks biden-
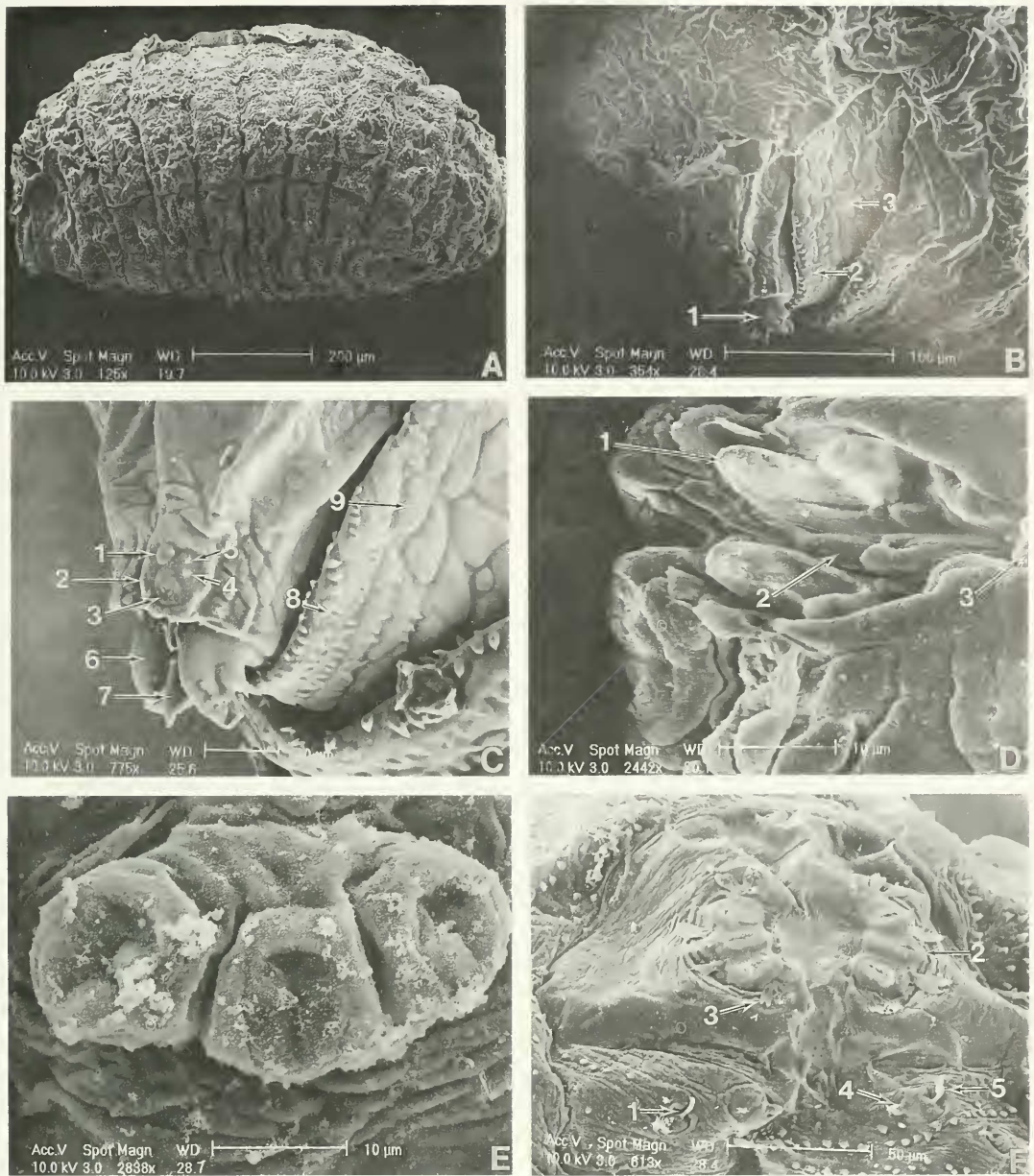
Fig. 3.   Second instar of *Trupanea vicina*: (A) habitus, anterior end to left; (B) gnathocephalon and prothorax, lateral view, 1- mouth hook, 2- minute acanthae, 3- rugose pad; (C) gnathocephalon, dorsolateral view, 1- dorsal sensory organ, 2- anterior sensory lobe, 3- terminal sensory organ, 4- lateral sensory organ, 5- supralateral sensory organ, 6- mouth hook, 7- median oral lobe, 8- minute acanthae, 9- rugose pad; (D) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe, 3- labial lobe; (E) anterior thoracic spiracle; (F) caudal segment, 1- stelex sensillum, 2- rima, 3- interspiracular process, 4- intermediate sensory complex, stelex sensillum, 5- intermediate sensory complex, medusoid sensillum.
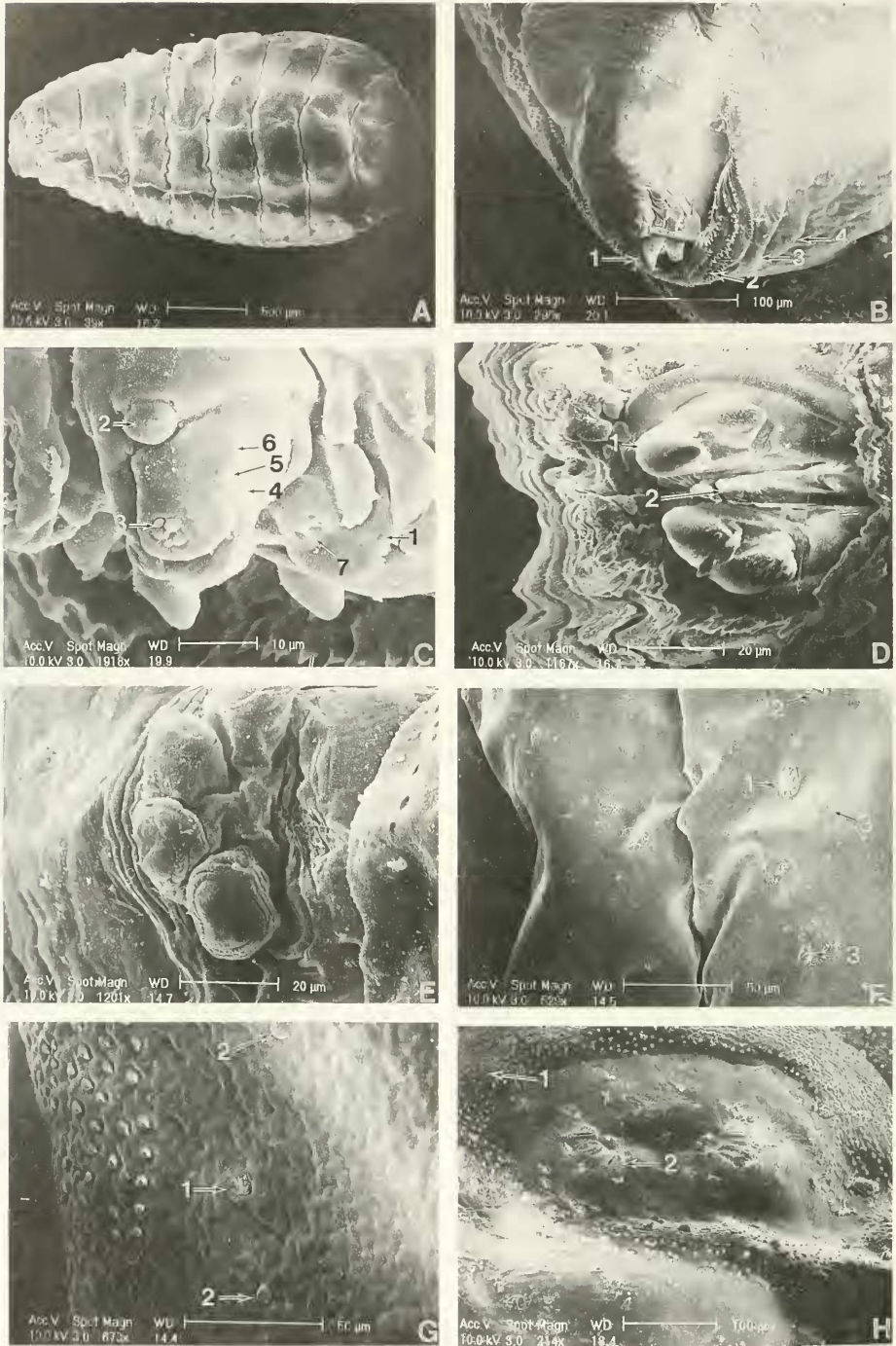
Fig. 4.   Third instar of *Trupanea vicina*: (A) habitus, anterior to left; (B) gnathocephalon and prothorax, anteriolateral view, 1- mouth hook, 2- minute acanthae, 3- rugose pad, 4- verruciform sensillum; (C) anterior sensory lobe, 1- serrated rugose pad, 2- dorsal sensory organ, 3- terminal sensory organ, 4- pit sensory organ, 5- lateral sensory organ, 6- supralateral sensory organ, 7- stomal sense organ; (D) gnathocephalon, ventral view, 1- mouth hook, 2- median oral lobe; (E) anterior thoracic spiracle; (F) meso- and metathorax (left to right), 1- spiracle, 2- stelex sensillum, 3- verruciform sensilla; (G) first abdominal segment, 1- spiracle, 2- verruciform sensilla; (H) caudal segment, 1- minute acanthae, 2- rima.
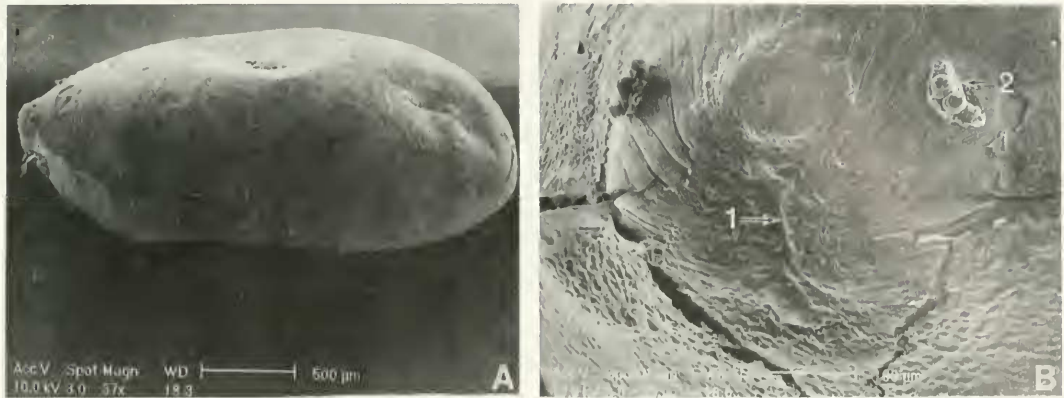
Fig. 5.   Puparium of *Trupanea vicina*: (A) habitus, anterior end to left; (B) anterior end, 1- invagination scar, 2- anterior thoracic spiracle.

tate (Fig. 4B-1, 4D-1); median oral lobe laterally flattened (Fig. 4D-2); prothorax circumscribed anteriorly with minute acanthae (Fig. 4B-2); rugose pads circumscribe prothorax posteriorad to acanthae (Fig. 4B-3); two rows of verruciform sensilla circumscribe prothorax posteriorad to rugose pads (Fig. 4B-4); anterior thoracic spiracle on posterior margin of prothorax bears 3–4 rounded papillae (Fig. 4E); mesothorax and metathorax not circumscribed anteriorly with verruciform sensilla (Fig. 4F); mesothoracic and metathoracic lateral spiracular complexes each consist of a spiracle (Fig. 4F-1), a stelex sensillum (Fig. 4F-2), and two verruciform sensilla (Fig. 4F-3); abdominal lateral spiracular complex consists of a spiracle (Fig. 4G-1) and two verruciform sensilla (Fig. 4G-2); caudal segment circumscribed by minute acanthae (Fig. 4H-1); two stelex sensilla, dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, ca. 0.03 mm in length (Fig. 4H-2), and four interspiracular processes, each with 2–3 branches, longest measuring 0.02 mm (seen but not shown); intermediate sensory complex consists of a medusoid sensillum and a stelex sensillum (seen but not shown).

The third instar bears serrated rugose pads similar to the third instars of *T. imperfecta, T. jonesi, T. nigricornis, T. pseudovicina, T. signata,* and *T. wheeleri* (Goe-

den and Teerink 1997b; 1998, 1999b; Goeden et al. 1998a; Knio et al. 1996a; Teerink and Goeden 1999). Unlike the third instars of 11 other *Trupanea* spp. examined that have tridentate mouth hooks (Goeden and Teerink 1997b, 1998, 1999a, b; Goeden et al. 1998a, b; Knio et al. 1996a; Teerink and Goeden 1998, 1999), the mouth hooks of the third instar of *T. vicina* are bidentate (Fig. 4D-1). Compared to three papillae in the second instar, the anterior thoracic spiracle of third instar bears 3–4 papillae (sometimes different on the same individual, Fig. 5B). Neither the meso- or metathorax are so circumscribed by verruciform sensilla; whereas, only the mesothorax is circumscribed in *T. nigricornis* (Knio et al. 1996a). Both the meso- and metathorax are circumscribed by verruciform sensilla in *T. arizonensis* and *T. imperfecta* (Goeden and Teerink 1999a, Teerink and Goeden 1999). The third-instar, metathoracic and abdominal spiracular complexes are identical to those of *T. imperfecta* (Teerink and Goeden 1999) and *T. wheeleri* (Goeden and Teerink 1999b). This is the first reported instance in which not only two, but three species of *Trupanea* share the same type and number of sensilla in the metathoracic and abdominal lateral spiracular complexes; the complexes of all nine other California *Trupanea* species studied have differed (Goeden and Teerink 1997b, 1998, 1999a; Goeden et al.

1998, 1999; Headrick and Goeden 1991; Knio et al. 1996a; Teerink and Goeden 1998, 1999). Other pairs of congeneric species in other genera are known to share the same number and type of sensilla in the lateral spiracular complexes, e.g., *Procecidochares kristineae* and *P. lisae; Aciurina idahoensis* and *A. michaeli; A. thoracica* and *A. trixa* (Goeden and Teerink 1996a, b. 1997a; Headrick and Goeden 1993; Headrick et al. 1997).

Puparium: Black, elongate-cylindrical, minute acanthae circumscribe intersegmental lines (Fig. 5A); anterior end bears the invagination scar (Fig. 5B-1) and anterior thoracic spiracles (Fig. 5B-2); caudal segment circumscribed by minute acanthae, two stelex sensilla, dorsad and ventrad of posterior spiracular plates; posterior spiracular plate bears three ovoid rimae, and four interspiracular processes, each with 2–3 branches; intermediate sensory complex (seen but not shown) consists of a medusoid sensillum and a stelex sensillum. Thirty-seven puparia averaged 2.87 ± 0.05 (range, 2.28–3.56) mm in length; 1.32 ± 0.02 (range, 1.00–1.56) mm in width.

DISTRIBUTION AND HOSTS

The distribution of *T. vicina* as mapped by Foote et al. (1993) included multiple locations in all States bordering Mexico, i.e., Arizona, California, New Mexico, and Texas, plus two locations in Nevada, and a single location in Georgia. The last record could represent a radical eastward extension of its range, perhaps resulting from its introduction along with marigold, one of more than 30 species of cultivated, aromatic, flowering herbs in the genus *Tagetes* originating in Mexico and widely cultivated in the Southwest (Bailey 1975). More likely, however, Gary Steck (in litt. 1998) suggests that the Georgia record for a single specimen collected in 1896 probably represents an error, as this would then be the sole record for this fly in the Southeastern U.S. during the past century.

Foote (1960) first reported *T. vicina* as

reared from marigold, which belongs to the subtribe Pectidinae in the tribe Helenieae of the Asteraceae (Hickman 1993, Bremer 1994). However, unlike *T. pseudovicina*, which is monophagous on *Porophyllum gracile* Bentham from this same tribe and subtribe in southern California (Goeden and Teerink 1998), *T. vicina* does not attack *P. gracile*, but has been reported by Goeden (1985, 1992) from four other genera and species of uncultivated ("wild"), native host plants belonging to the Pectidinae and Helenieae in southern California, i.e., *Adenophyllum* (= *Dyssodia*) *porophylloides* (A. Gray) Strother, *Thymophylla pentachaeta* var. *belenidium, Nicolletia occidentalis* A. Gray, and *Pectis papposa* Harvey and A. Gray var. *papposa*, as listed by Hickman (1993).

A quandary is presented by the host record dating from 1982 for three females of *T. vicina* from *Coreopsis douglasii* (deCandolle) H.M. Hall in Goeden (1985), a genus from which this tephritid since has never again been reared, even during intensive and extensive field study of two principal tephritid associates of *Coreopsis* spp., *Dioxyna picciola* (Bigot) (Headrick et al. 1996) and *T. jonesi* (Goeden et al. 1998a). This host record for *T. vicina* is suspect, or at least atypical, because *Coreopsis* belongs to an entirely different tribe of Asteraceae, the Heliantheae, subtribe Coreopsidinae (Bremer 1994). The identity of these three specimens, still in the research collection of RDG, has been reconfirmed. Possible explanations include contamination of the sample with flower heads accidentally collected from an intergrown or nearby host plant, or oviposition mistakes by a female *T. vicina*, suspected to have occurred with at least one other, congeneric, sympatric, stenophagous (narrow host range), desert tephritid, *T. pseudovicina* (Goeden and Teerink 1998). Also like several other tephritid species that we have studied, i.e., *Trupanea conjuncta* (Goeden 1987), *T. pseudovicina* (Goeden and Teerink), *Tomoplagia cressoni* Aczél (Goeden and

Headrick 1991), and *Zonosemata vittigera* (Coquillett) (Goeden and Ricker 1971), *Trupanea vicina* represents a native southern California tephritid closely associated with native host-plants primarily distributed in Mexico and southward, where they remain little studied.

BIOLOGY

Egg.—In 31 closed, preblossom, immature flower heads of *Tagetes* sp., 27 (66%) of 41 eggs were inserted between or through the tips of the phyllaries and parallel to and between the florets; the remainder were oviposited through the phyllaries laterally and deposited loosely atop the florets and parallel to the receptacle in the conical space beneath the appressed apices of the phyllaries (Fig. 6A). All eggs were oviposited pedicel-last. Only three (10%) of 31 flower heads with eggs respectively contained 5, 1, and 2 florets damaged by ovipositional probing; no eggs were inserted into plant tissues. The diameters of the receptacles of 31 flower heads containing eggs averaged 2.9 ± 0.1 (range, 1.9–3.7) mm, and these heads contained an average of 1.5 ± 0.1 (range, 1–3) eggs, all oviposited singly. If more than one egg was found in a head, they were always separated, and thus, probably oviposited by different females.

Larva.—Upon eclosion, first instars tunneled into the apical end of an unelongated floral tube of an immature floret (Fig. 6B). An average of 1.3 ± 0.2 (range, 1–2) first instars was found feeding within eight, closed, preblossom, marigold flower heads, the receptacles of which averaged 3.2 ± 0.1 (range, 2.8–4.0) mm in diameter. These infested heads contained an average of 61 ± 3 (range, 48–78) florets, of which an average of only 1.9 ± 0.5 (range, 1–5) floral tubes, or 3.2% (range, 1.3–8.9%), were damaged. First instars continued to feed down the floral tubes towards the ovules. No ovules or receptacles within these eight infested flower heads were abraded or pitted by first-instar feeding.

Second instars fed mainly in ovules of preblossom marigold flower heads or in soft achenes of open heads (Fig. 6C). Most second instars fed separately with their mouthparts directed towards the receptacles within adjacent ovules/soft achenes, but well above the receptacles (Fig. 6C). Receptacles of 21 flower heads containing second instars were undamaged and averaged 3.9 ± 0.1 (range, 2.9–4.7) mm in diameter. These flower heads contained an average of 1.6 ± 0.3 (range, 1–6) second instars that had destroyed an average of 7.1 ± 1.1 (range, 2–26) ovules/soft achenes, or 11.7% (range, 3.1–34%) of an average total of 61 ± 3 (range, 38–83) ovules/soft achenes per head.

Most third instars confined their feeding to soft achenes in the centers of open or postblossom flower heads of marigold (Fig. 6D) and *Thymophylla pentachaeta* (Fig. 6E). In 18 marigold flower heads (Fig. 6D) averaging 3.6 ± 0.1 (range, 2.3–4.6) mm in diameter and containing an average of 1.4 ± 0.2 (range, 1–4) third instars, an average of 11.4 ± 1.0 (range 1–26) soft achenes were damaged, or 23% (range, 5–67%) of an average total of 56 ± 4.2 (range 21–110) soft achenes per head. In 42 smaller flower heads of *T. pentachaeta* (Fig. 6E) averaging 1.4 ± 0.02 (range, 1.1–1.7) mm in diameter and each containing an average total of 72 ± 2.1 (range 46–105) soft achenes and one third instar, an average of 26.5 ± 0.9 (range 16–38) soft achenes were damaged, or 37.5% (range, 25–52%). Third instars in flower heads of both hosts fed with their long axes oriented perpendicular to and mouthparts directed towards the receptacles (Fig. 6E). Only 2 (4.7%) of 42 receptacles in *T. pentachaeta* were pitted by third instar feeding; none in 18 infested marigold flower heads. Upon completing their feeding, the larvae oriented with their anterior ends away from the receptacles, retracted their mouthparts, and pupariated (Fig. 6F).

Pupa.—Flower heads containing puparia (Fig. 6F) reflected the greatest damage produced by the seed-feeding larvae of *T. vi-*
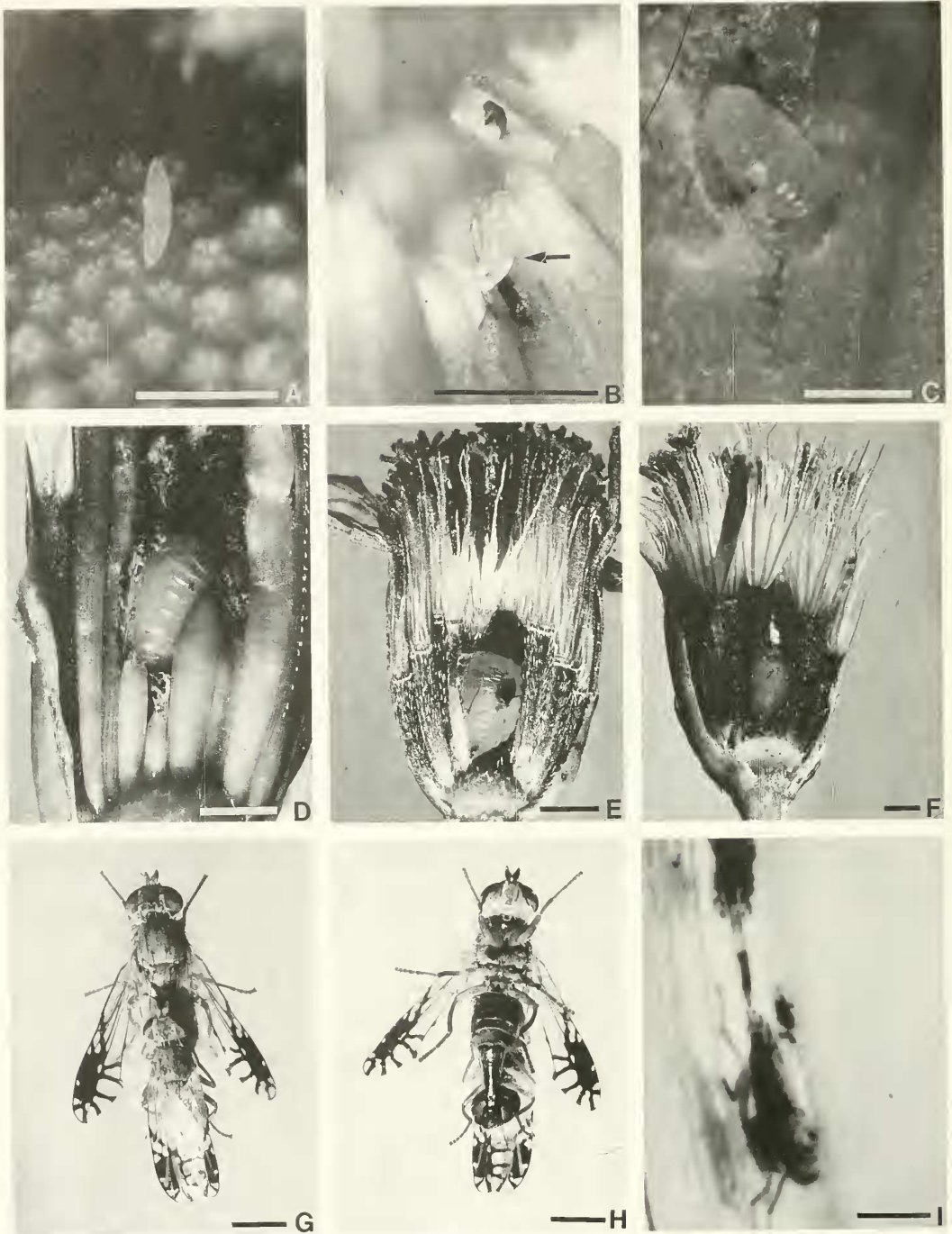
Fig. 6.   Life stages of *Trupanea vicina*: (A) egg laid atop florets in immature flower head of marigold, (B) early first instar (arrow) feeding at apex of floret in marigold, (C) second instar feeding in floral tube and ovule in flower head of marigold, (D) third instar feeding on ovules in flower head of marigold, (E) third instar feeding among soft achenes in center of open flower head of *Thymophylla pentachaeta*; (F) puparium in flower head of *T. pentachaeta*, (G) mating pair, dorsal view; (H) mating pair, ventral view; (I) male withdrawing aculeus at termination of mating (blurred because entire process took only 3–4 sec, see text). Lines = 1 mm.

cina within flower heads sampled. The receptacles of 34 infested marigold flower heads containing puparia averaged 3.6 ± 0.2 (range, 2.3–8.2) mm in diameter and bore an average total of 53.9 ± 1.6 (36–73) soft achenes/florets, of which an average of 15.3 ± 1.2 (range, 4–35) soft achenes/florets or 29% (range, 7–78%) were damaged. The receptacles of 12 (35%) of the 34 flower heads were pitted. These 34 heads contained an average of 1.5 ± 0.2 (range, 1–4) puparia. All puparia of *T. vicina* were found in the center of the flower heads with their anterior ends facing away from the receptacles and their long axes perpendicular to the receptacles (Fig. 6F).

Adult.—Adults emerged from mature flower heads, and were long-lived under insectary conditions, as unmated males averaged 94 ± 8 (range, 14–147) days, and virgin females averaged 72 ± 6 (range, 29–130) days. Such longevities are commensurate with the aggregative type of life cycle ascribed below to this tephritid.

The premating and mating behaviors of *T. vicina* were not studied in the field, but we did study these behaviors using petri dish arenas found to be so useful with many other noncongeneric, nonfrugivorous, tephritid species (Headrick and Goeden 1994). Unlike most other *Trupanea* spp. that we have studied, at least two matings of *T. vicina* were observed in these arenas, but only when more than single pairs of flies were caged together. This crowding factor should be addressed experimentally with other *Trupanea* spp. Before we began our use of petri dish arenas, mating under crowded conditions also was observed in mass sleeve-cagings of *T. bisetosa* adults (Cavender and Goeden 1982). Premating behaviors observed with *T. vicina* were abdominal pleural distensions by males (Headrick and Goeden 1994, Knio et al. 1996b, Goeden et al. 1998a) and wing hamations combined with supinations as reported for *T. jonesi* (Goeden et al. 1998a), but without rapid wing vibrations, by both sexes. Two matings (Fig. 6G, H) were observed during the early afternoon with different pairs of flies of 25- and 28-min duration; similarly short mating duration have been reported for all congeners studied to date (Cavender and Goeden 1982, Goeden et al. 1998a, Headrick and Goeden 1994, Knio et al. 1996b). Each pair apparently mated only once, as reported with *T. jonesi* (Goeden et al. 1998a). The copulatory position of each pair of *T. vicina* was as described for *T. jonesi* (Goeden et al. 1998a). Disengagement, rarely observed in *Trupanea* spp. (Headrick and Goeden 1994, Knio et al. 1996b, Goeden et al. 1998a), was seen once and involved a male turning 180° as he rapidly dismounted and walked away from the female while pulling free his genitalia, all in 3–4 sec. (Fig. 6I). As with other *Trupanea* spp., no post-copulatory behavior was observed other than individual groomings by both flies, and as the male recoiled his genitalia.

Seasonal history.—The life cycle of *T. vicina* in southern California follows an aggregative pattern in which the long-lived adults overwinter while in reproductive diapause and then aggregate to mate on pre-blossom host plants in the spring (March–April) (Headrick and Goeden 1994). They reproduce limitedly at first on wild hosts, e.g., *Adenophyllum porophylloides*, in the low-elevation Colorado Desert, then in the higher-elevation, Mojave Desert, and on occasional host plants scattered in chaparral of the interior valleys (Munz 1974, Hickman 1993). However, the major host plants on which *T. vicina* reproduces in southern California are various varieties of herbaceous, cultivated marigold, widely planted as summer annuals. This tephritid conceivably produces three to four overlapping, nondiscrete generations on marigold from early summer (June) until as late as November, or until frost occurs. Fortunately, for both gardeners and *T. vicina*, there is no loss of ornamental quality to infested marigold flower heads, and thus no need for chemical control, because most feeding and pupariation occur in the mature heads nor-

mally pruned or left to dry and abscise. Thus, like *T. signata* (Goeden and Teerink 1997b), this native tephritid species has adapted to and benefited from human floricultural practices.

Natural enemies.—*Pteromalus* sp. (Hymenoptera: Pteromalidae) was reared from mature flower heads of *Adenophyllum porophylloides* bearing third instars and puparia as a probable solitary, larval-pupal endoparasitoid of *T. vicina*.

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